

COVER ILLUSTRATION

A choroidal sleight of hand

Nocturnal mammalian flight began in the early Eocene night approximately 52–55 million years ago when few competitors for the feast of nocturnal insects and flowering plants existed. Bats! Highly successful and almost pan-continental, these extraordinary creatures have radiated into two major families—the microchiroptera (microbats) and mega-chiroptera (megabats). Considered blind, perhaps, because they were thought to navigate successfully without eyesight, bats are far from blind. Megabats are crepuscular (dusk and dawn) or nocturnal in habit and microbats are strictly nocturnal, with visual adaptations that address those niches.

While the microbats comprise the echolocating families, the megabats consist of frugivorous and nectarivorous bats. The phylogeny of these two groups of bats remains controversial, with a wide range of hypotheses about their relationship, including “flying primates” and “deaf fruit bats.” The fruit bats have better vision, and have evolved olfactory skills that rival those of dogs.

The tube-nosed fruit bats, like *Nyctimene robinsoni* (the eastern tube-nosed fruit bat), have evolved a stereo olfaction system that will locate an odour plume three dimensionally and follow it. Tube-nose fruit bats are specialists, preferring figs, but will feed on other fruit. Being specialists, they must be able to follow scent through the eastern Australian rainforest where they are native. Although it seems counter-intuitive, odours tend to remain in distinct trails, called “odour plumes,” especially in a rain forest, which is less affected by wind currents. Odours do diffuse to some extent, but usually provide distinct plumes that can be followed, especially by a creature such as *N. robinsoni* that is well equipped with a stereo nose and enlarged olfactory bulbs.

Vision in the bat illustrated on this month's cover has not been specifically evaluated, but vision in closely related species has. The retina is composed primarily of rods, as you might expect of a crepuscular animal, but cones do exist. Some megabats have been shown to have the potential for trichromatic vision by molecular analysis of opsin

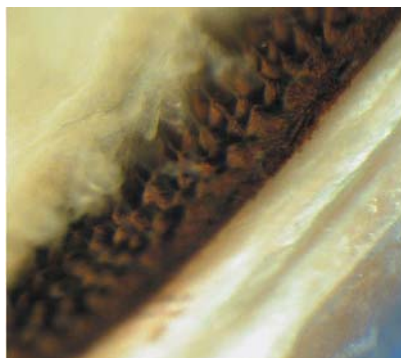


Figure 1 Choroid exposed.

genes. The visual pigments that provide colour vision for fruit bats include a short wavelength opsin with sensitivity that extends into the ultraviolet and a long wavelength opsin with sensitivities that could clearly be described as red. Fruit bats probably use their colour vision to help discern coloured fruit or blossoms. In crepuscular light, using their rods as a third visual pigment, there may even be some form of, or interpretation of, trichromacy since there would be three different peaks of sensitivity to wavelengths of light. Evidence suggests that the ultraviolet opsin is active and that bats do see into this range, which is most unusual for a mammal. For example, phakic humans cannot see into this range because our crystalline lenses, and those of most pseudophakes, block ultraviolet light.

The eye of the fruit bat is distinct, though, as there is no retinal vasculature, and the retinal layering is surprisingly thick, up to perhaps 250 µm, or more. Choroidal oxygen and nutrients would not diffuse much more than 140 µm. So, how do fruit bats nourish their inner retina?

The choroid consists of spike-like projections that stud the retina much like rivets uniting two pieces of metal (fig 1). As can be seen from the right side of the cover, this creates a texture or undulations in the retina. These projections are called papillations. The tip of each choroidal papilla projects 125–150 µm into the retina and is believed to nourish the surrounding tips of the inner retina so that no portion of retina is much more than 100 µm from its blood supply. This eliminates the

need for a retinal vascular system, and helps improve the image, since these bats don't have to look through their own blood supply.

But, what does this do to the retinal image? Apparently nothing, or at least the bats seem adjusted to it. Fruit bats have an area centralis, but no true fovea. The visual acuity of fruit bats ranges from 3–6 cycles per degree which is approximately equivalent to that of a cat. Although their diurnal vision is not as good as ours, fruit bats do use vision to locate fruit and blossoms, as their nocturnal vision is excellent. Even the microbats are known to use visual cues for larger prey, especially when echolocation would not be useful in prey detection. Vision in the microbats, however, is approximately 1–2 cycles per degree, somewhat less than a rodent.

The visual image, and hence visual processing, in fruit bats must be different from other mammals since these papillae create an undulating retina. This would serve to increase the number of photoreceptors, improve light gathering ability, and perhaps increase depth of field, but may require a different form of retinal processing or cerebral integration. The dioptric difference between the peaks and depressions of the choroidal papillae is approximately 1.5 dioptres, and early investigators suggested that this difference between the peaks and valleys allows the bat to be in focus at distance and near simultaneously. Other early investigators suggested that the fruit bats could not accommodate. Both of these assertions are not true, as these bats can accommodate at least 3.5 dioptres and don't need these choroidal papillae for near focusing.

These choroidal papillae, then, appear to be a sleight of hand for oxygen delivery.

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Image of *Nyctimene robinsoni* on left of cover by Jack Pettigrew, MD.

Histological images on right of cover and this page by William Lloyd, MD.